RESEARCH ARTICLE

Patching up the past one fossil at a time: A new genus and species of Eulophidae from Eocene Baltic Amber (Hymenoptera, Chalcidoidea)

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Abstract

A new fossil species of Eulophidae, *Kressleinius celans*, **gen. et sp. nov.**, is described from Eocene Baltic amber. It does not place into any extant genera within Eulophidae due to a lack of distinctive synapomorphies. The results of a morphology-based phylogenetic analysis placed *K. celans* in Tetrastichinae because of features shared with several genera, including having 6 flagellomeres past the anelli, admarginal setae short, propleura diverging, and a newly described feature of the transepimeral sulcus. This represents the oldest known fossil for the largest family of Chalcidoidea in terms of described species.

Keywords

Introduction

Chalcidoidea (Hymenoptera) is a group of parasitoid wasps that are ecologically and economically important, providing control of pests that damage a number of agriculturally important crops (Heraty 2009; Heraty et al. 2013). Over 22,000 species of

Chalcidoidea, with a high diversity of molecular and morphological attributes, have been described; however, as many as 500,000 species are estimated (Heraty et al. 2013; Noyes 2019). The vast majority of Chalcidoidea are undescribed and their fossil record, dating back to the late Cretaceous (Yoshimoto 1975; Poinar and Huber 2011; Gumovsky 2018), is very poorly known despite numerous specimens being present in various amber deposits.

Eulophidae, the largest family within Chalcidoidea in terms of described species, occurs on all continents, except Antarctica (Burks et al., in prep). It currently has five subfamilies, Entedoninae, Entiinae, Eulophinae, Opheliminae, and Tetrastichinae, all with a convoluted taxonomic history (Ashmead 1904; Graham 1959; Bouček 1988; Gauthier et al. 2000; Gumovsky 2002; Burks et al. 2011). It has a massive range of reproductive strategies, including attacking species from at least 10 insect orders, spider eggs, and even galls formed by nematodes and mites (Schauff et al. 1997). Within Eulophidae, Tetrastichinae uses the broadest range of reproductive strategies, from phytophagy to hyperparasitism (Kosheleva and Kostjukov 2014). Despite the current abundance and high diversity of Eulophidae, there are only two verified fossils, *Chrysonotomyia dominicana* Gumovsky and an undescribed fossil from *Achrysocharoides* Girault (Gumovsky 2001), described from Miocene Dominican amber (15–20 Ma, Iturralde-Vinent and MacPhee 1996) within Entedoninae.

Here we describe a new eulophid fossil from Eocene Baltic amber (38–47 Ma, Ritzkowski 1997), representing the oldest known fossil for the family. The fossil is tentatively placed in Tetrastichinae, a diverse subfamily currently with 110 genera that have been sparsely sampled molecularly (Burks et al. in prep). Morphologically this group has a distinctive gestalt based on characteristics such as complete incised notauli on the mesoscutum, and parallel submedian grooves on the mesoscutellum. Even though these characteristics can be diagnostic for Tetrastichinae, they are homoplastic and can be shared with species in Eulophinae. As a result, placing the specimen in either Tetrastichinae or Eulophinae can prove difficult since they share several apparent plesiomorphies aside from particular characteristics of the tribes. Features defining the subfamilies have not been well defined, and often the subfamilies are more easily recognized by identifying the specimen to genus because they can be characterized more precisely. Character support has not been strong and only through molecular or combined morphological and molecular studies has monophyly of both subfamilies and tribes been resolved (Gauthier 2000; Burks et al. 2011; Gumovsky 2011; Munro 2011; Heraty et al. 2013; Rasplus et al. in prep). Here we focus on morphology for placement of our fossil.

Methods

The single specimen (holotype) is from the Staatliches Museum für Naturkunde, Stuttgart (**SMNS**). Photographs were taken using a Leica Imaging System with a Z16 APO A microscope and all scale bars in photos are in millimeters. Most morphological

terminology follows Heraty et al. (2013). We provide two new terms for sulci on the head: ocs = ocellar triangle sulcus = a sulcus that encircles the ocellar triangle, and oos = ocellar-ocular sulcus, a sulcus that is a line touching the edge of the eye and connecting to the ocs.

A character matrix for phylogenetic analysis was constructed in Mesquite (Maddison and Maddison 2018). Voucher specimens were chosen from those used in an ongoing anchored enrichment molecular study. Some taxa were added for better coverage of Tetrastichinae. The matrix was analyzed using parsimony in the phylogenetic analysis program PAUP4.0* (Swofford 2019). To reduce the number of competing most-parsimonious trees, we used Successive Approximations Character Weighting (SAW) using the character retention index, a base weight of 1,000 and repetitive iterations of reweighting until tree weights stabilized (Carpenter 1988; Heraty 2002); on the final trees, character weights were set to one and the tree length was compared to the most parsimonious unweighted search trees. Results were summarized using a strict consensus tree. Bootstrap values were obtained by resampling 1,000 replicates using unweighted characters.

Morphological characters

Certain characters were chosen to test morphological reasoning for placement of the fossil species. The character matrix can be accessed on Dryad Data Repository (DOI https://doi.org/10.6086/D19098). Some features that could not be assessed on the fossil were chosen to ensure that subfamily monophyly resembled that of recent phylogenies (Gauthier et al. 2000; Burks et al. 2011; Gumovsky 2011; Heraty et al. 2013).

1. Antennal flagellomere formula excluding anelli (in format of funiculars, clavomeres): 0 = 6,1; 1 = 6,2; 2 = 2,3 (Fig. 4C); 3 = 5,3; 4 = 3,1; 5 = 3,3 (Fig. 4A); 6 = 4,2 (Fig. 4B).

Flagellomere count proved to be problematic to assess, due to a poor visible distinction between having one or more anelli in Tetrastichinae and Opheliminae. However, it was observed that some taxa possessed an almost constant count of funiculars and clavomeres beyond the anelli. Funiculars are loosely articulated segments between the anellus and clava, whereas the clava is comprised of closely appressed and immobile terminal segments (Heraty et al. 2019). The combination of funiculars and clavomeres were necessary to separate Cirrospilini from Tetrastichinae. Members of Cirrospilini have 2 funiculars and 3 clavomeres or 3 funiculars and 2 clavomeres (Fig. 4C, D), whereas members of Tetrastichinae have 3 funiculars and 3 clavomeres (Fig. 4A). The formula was coded only for females, because many Eulophidae are sexually dimorphic for this character, generally possessing one additional funicular in males.

2. Antennal flagellomere count beyond anelli: coded as actual count.

This character is the raw count of funiculars plus clavomeres, regardless of their arrangement.

3. Frontal sulci of head: 0 = with a complex of sulci: V-shaped connecting to scrobal sulci, but not connecting to ocs (Burks et. al. 2011, fig. 18); 1 = without sulci; 2 = with a single transverse sulcus near mid-height of face (Gauthier et al. 2000, fig. 8D); 3 = scrobal sulci merging and proceeding to a small curved sulcus immediately ventral to ocellar triangle (Fig. 5A); 4 = with a complex of sulci: V-shaped connecting to scrobal sulci and connecting to a sulcus encircling the ocellar triangle (Fig. 5B).

Exact homology of frontal sulci proved difficult to establish with certainty, but particular classes of sulci could be established. State 1 occurs mainly in Entiinae, with sporadic and presumably homoplastic appearances in other subfamilies. State 2 occurs in most Cirrospilini but not in other eulophids (Gauthier et al. 2000). State 0 occurs in many Entedonini, where a V-shaped sulcus is often present distant from the ocelli. State 4 occurs in many Tetrastichinae (LaSalle 1994). The scrobal sulci in Tetrastichinae are separated in a few taxa, such as *Crataepus* Förster and *Pronotalia* Gradwell, but the parascrobal areas of most tetrastichines seem to be enlarged and meeting medially to conceal the median areas from view (LaSalle 1994). This feature could not be seen in the fossil species due to face collapse, but a collapsed face is expected to occur only in taxa that have frontal sulci.

4. Propleuron shape: 0 = posteriorly angular (Gauthier et. al. 2000, fig. 7B); 1 = posteriorly straight (Gauthier et. al. 2000, fig. 7A).

State 1 was reported by Gauthier et al. (2000) as diagnostic for most Eulophini. This state also occurs in presumably unrelated taxa such as the pteromalid subfamily Cerocephalinae, but nearly all other chalcidoids possess state 0.

5. Prepectus dorsal length: 0 = same length or shorter than acropleuron; 1 = longer than acropleuron (Fig. 1E).

The fossil species was observed to have a large prepectus. While this is a homoplastic feature throughout Eulophidae, it was coded because it was one of the few distinctive features of the fossil species. Most Eulophidae have a smaller prepectus, but large-bodied species are likely to have a larger prepectus relative to the surrounding sclerites. The acropleuron was chosen for this comparison because in Eulophidae it is near the prepectus and relatively uniform in relative length.

6. Mesothoracic spiracle visibility: 0 = exposed to view externally (Fig. 3D); 1 = concealed by pronotum and mesoscutum (Gumovsky 2011, fig. 6F).

Gumovsky (2011) used state 1 to help define the tribe Entedonini. Most other Eulophidae, and most other Chalcidoidea, have an exposed mesothoracic spiracle, although *Anselmella* Girault (Anselmellini, currently unplaced within Eulophidae) was also observed to have a concealed spiracle.

7. Mesoscutellar submedian grooves: 0 = absent (Fig. 3F); 1 = present (Fig. 3E).

Various Eulophidae have submedian grooves (occurring medial to the paired mesoscutellar setae), a feature found in almost no other Chalcidoidea. The mesoscutellum was not easily visible in the fossil species, but this feature was coded to help separate

taxa that lack these grooves, such as Entiinae and Opheliminae, from taxa that generally have them. These grooves are posteriorly subparallel in taxa such as Cirrospilini and most Tetrastichinae. A U-shaped, posteriorly-meeting groove (state 1) (Burks et. al. 2011 fig. 26) is shown to be autapomorphic according to our matrix, and present only in *Elachertus cacoeciae* Howard (Eulophini).

8.   Transepimeral sulcus presence: 0 = absent (Fig. 5D); 1 = present (Fig. 3A–D).

The transepimeral sulcus was one of the few reasonably distinctive features of the fossil species that could be assessed without doubt. While nearly all eulophids have a transepimeral sulcus, *Anselmella* and the outgroup species *Foersterella erdoesi* Bouček (Tetracampidae) do not.

9.   Transepimeral sulcus shape: 0 = arched or sinuate and extending dorsoventrally (Fig. 3C); 1 = arched or sinuate and extending anteroposteriorly (Fig. 3D); 2 = straight (Fig. 3A, B).

A strongly curved transepimeral sulcus was found to separate many Eulophinae from many Tetrastichinae, with few exceptions. In the two Entedonini coded, the transepimeral sulcus extends posteriorly from near the middle of the mesopleural sulcus, which was coded as a characteristic 10, transepimeral sulcus junction with mesopleural sulcus, state 1 because of its difference in connection of the sinuate sulci in other taxa. Inapplicable characteristics, where no sulcus was present were coded as "?".

10. Transepimeral sulcus junction with mesopleural sulcus: 0 = meeting at mesocoxal insertion (Fig. 3A); 1 = meeting far dorsal to mesocoxal insertion (Fig. 3D).

The junction of the transepimeral sulcus with the mesopleural sulcus was shown to be an interesting feature to help differentiate eulophid subfamilies. While this character is homoplastic across Eulophinae and Tetrastichinae, state 0 was unequivocally present in the fossil species, and therefore this character was used to help place it. Taxa without a sulcus were coded as "?".

11. Admarginal setae presence: 0 = present (Fig. 2A, B); 1 = absent.

Admarginal setae are located immediately posterior to the fore wing marginal vein and are frequently longer than the surrounding dorsal and ventral setae. Most Eulophidae have these setae, but they are absent in a few, presumably derived, species.

12. Admarginal setae length: 0 = long (Graham 1959 fig. 9); 1 = short (Fig. 2A, B).

The distinction of admarginal setae occurs mainly in two ways, either by being very different in length relative to surrounding setae, or by their isolation. In many Eulophidae, the admarginal setae are much longer than most other fore wing setae. Both states occur in other Chalcidoidea, with state 1 being arguably the most frequent. Taxa without admarginal setae were coded as "?".

13. Number of rows of admarginal setae: 0 = more than one row (Fig. 2A, B); 1 = one row (Graham 1959, fig. 9).

In many Eulophinae, long admarginal setae are present in only one row. This is also the case in taxa where the admarginal setae arise in part from the ventral surface of the marginal vein, such as Opheliminae. When multiple rows are present, they may occur irregularly as 2 or 3 rows, sometimes with the two fore wings differing. Taxa without admarginal setae were coded as "?".

14. Cubital fold shape: 0 = straight or only slightly curved (Graham 1959, fig. 7); 1 = strongly curved near basal fold (Graham 1959, fig. 6).

A strong curvature of the cubital fold, and of its corresponding setal track, is known in Cirrospilini (Graham 1959). It proves diagnostic for many members of the tribe, although some species possess only a mildly curved cubital fold.

15. Parastigma connection: 0 = smooth (Graham 1959, fig. 5); 1 = abrupt (Graham 1959, figs 8–9).

The abruptness of the connection of the parastigma with the marginal vein has often been used to identify Eulophini (Graham 1959), although we found it to be difficult to assess in many species.

16. Postmarginal vein length: 0 = as long or longer than stigmal vein (Fig. 2A, B); 1 = shorter than stigmal vein (LaSalle 1994, figs 129–130).

The postmarginal vein is variable in length in Eulophidae, although a majority of taxa possess either state 0 or state 1. While most Tetrastichinae have state 1, *Peckelachertus* Yoshimoto and *Quadrastichodella* Girault have state 0.

17. Tarsomere count in females: 0 = 5; 1 = 4.

The number of tarsomeres in females is diagnostic for Eulophidae, with four tarsomeres instead of the usual five. This character separates the outgroup species *F. erdoesi* (Tetracampidae) from the ingroup Eulophidae.

18. Propodeal callus setae: 0 = 10 or more setae (Fig. 4F); 1 = 0 to 9 setae (Figs 4E, 5C).

Larger numbers of propodeal callus setae are present in most Eulophini. Additional states were initially coded for taxa with a smaller number of propodeal callus setae, but these proved to be more difficult to treat consistently and thus were collapsed into state 1.

Taxonomy

Kressleinius Domer & Burks, gen. nov.
http://zoobank.org/AAEB91C6-56FC-4A22-B870-A87C1BEB228F
Figs 1A–2A

Type species. *Kressleinius celans* Domer & Burks, sp. nov.
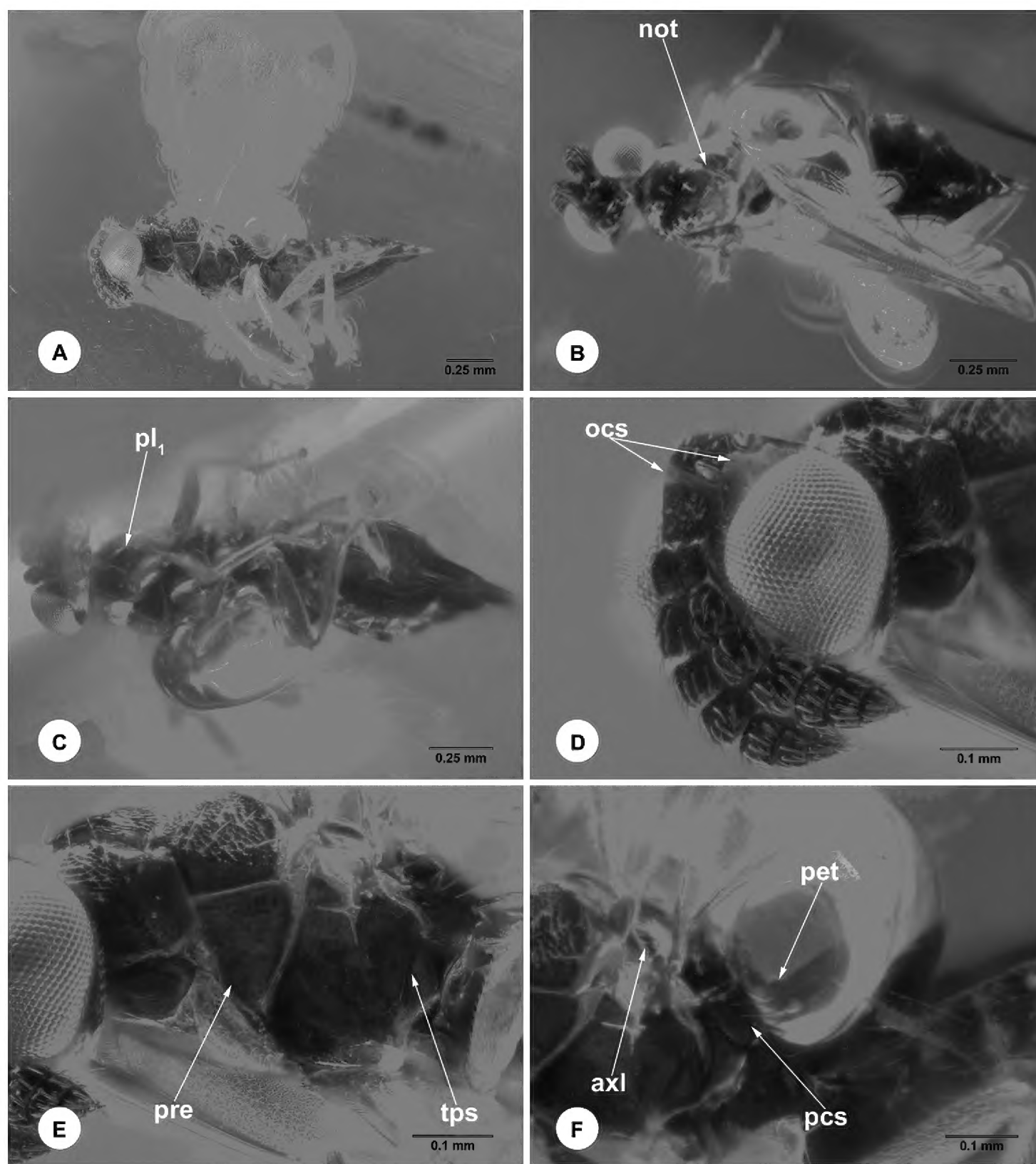
Figure 1. A–F. *Kressleinius celans* gen. et sp. nov., holotype female (SMNS BB-2847) **A** habitus **B** habitus, dorsal view, not = notaulus **C** body, ventral view, pl₁ = propleuron **D** antenna, ocs = ocellar triangle sulcus **E** mesosoma, lateral, pre = prepectus, tps = transepimeral sulcus **F** mesosoma, oblique lateral, axl = axillula, pcs = propodeal callus setae, pet = petiole.

Diagnosis. This genus differs from other genera in Tetrastichinae by a combination of the following characteristics. Eye setose. Malar sulcus present and only slightly arched. Sulcus encircling ocellar triangle (Figs 1D, 5B, ocs) and extending to eyes (Figs 1D, 5B, oos). Antenna with 1 anellus, 3 funiculars, and 3 clavomeres. Prepectus large, about twice as long as acropleuron, and subtriangular. Transepimeral sulcus straight, extending dorsoventrally, meeting pleural sulcus at metacoxa. Propodeal
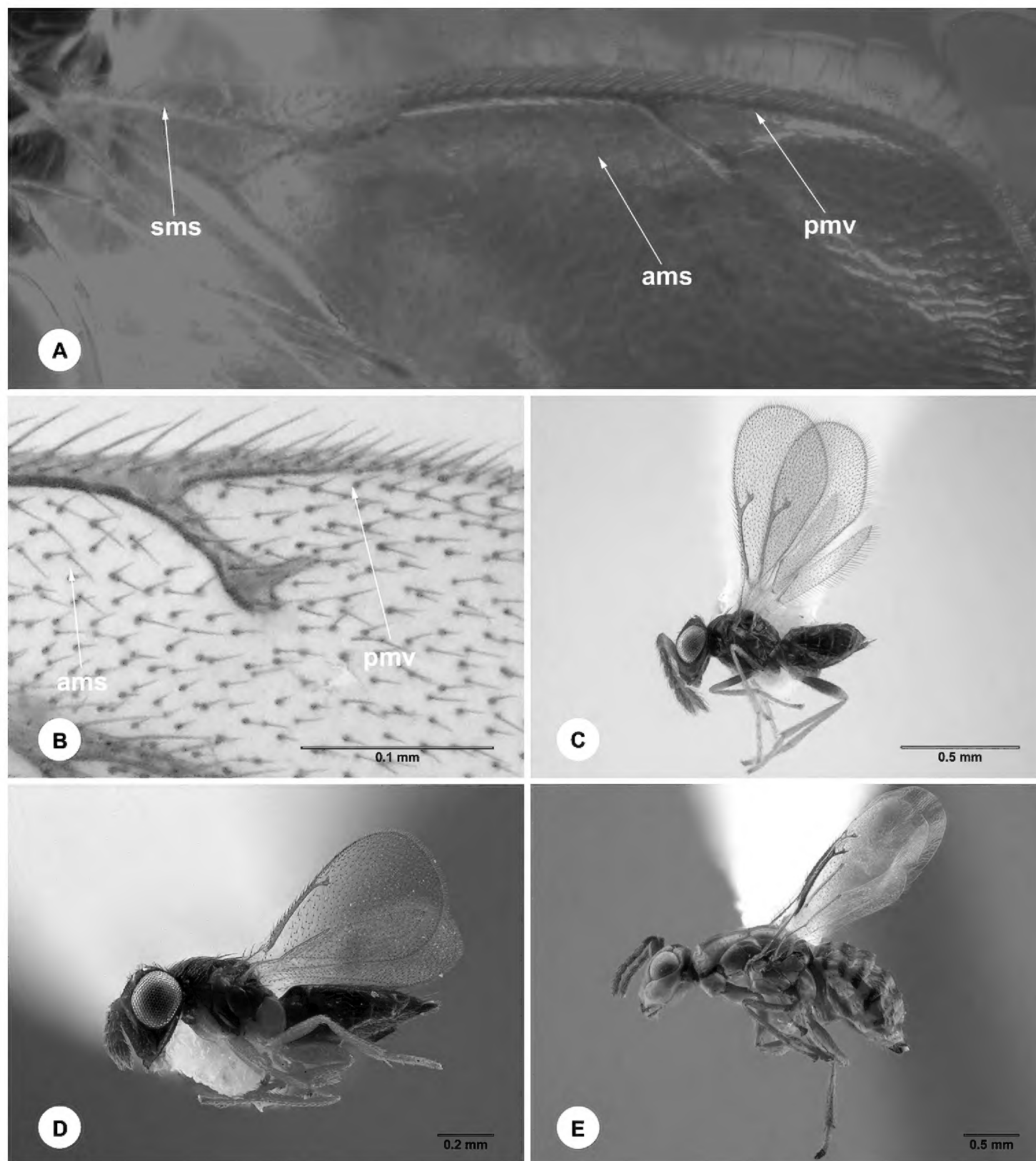
Figure 2. A–E. A *Kressleinius celans* gen. et sp. nov., holotype female, fore wing venation, pmv = postmarginal vein, ams = admarginal setae, sms = submarginal vein setae **B, C** *Peckelachertus* sp.: **B** fore wing **C** habitus **D** *Nesolynx* sp. habitus **E** *Quadrastichodella* sp., habitus.

callus with 5 setae. Postmarginal vein longer than stigmal vein, submarginal vein with 6 setae. Cercal setae subequal in length.

Description. *Head* with eye setose; sulcus encircling the ocellar triangle and extending to eyes; malar sulcus present and only slightly arched; maxillary and labial palps 1 segmented; antenna with 1 anellus, 3 funiculars, and 3 clavomeres.

Mesosoma with prepectus large and subtriangular, its dorsal length twice acropleuron length; mesoscutal median sulcus absent. Notauli complete, straight, incised. Axillae advanced. Mesopleural sulcus slightly curved, meeting transepimeral sulcus
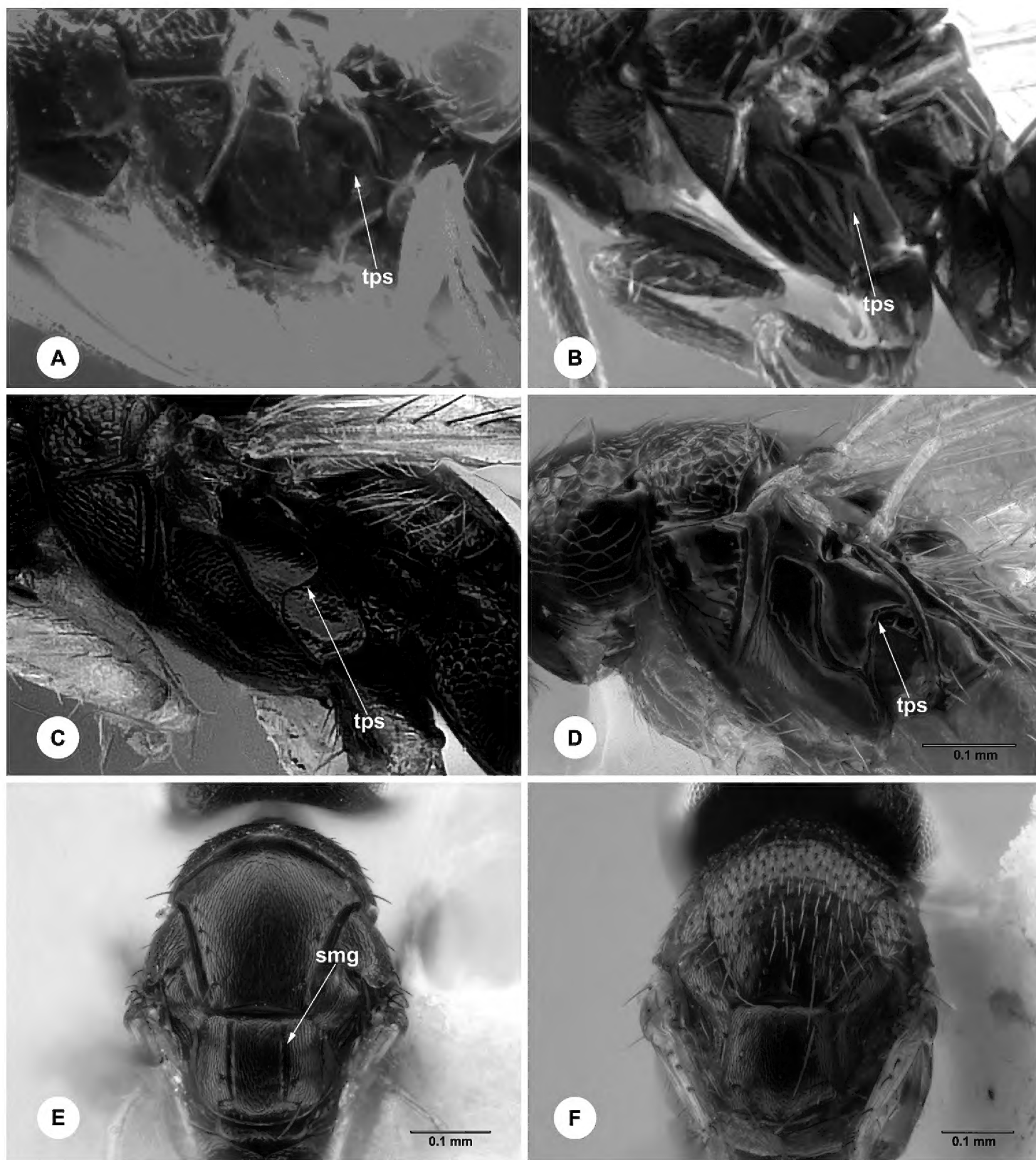
Figure 3. A–F. A *Kressleinius celans* gen. et sp. nov. holotype female, mesosoma, lateral, tps = transepimeral sulcus **B** *Aprostocetus hibus*, mesosoma, lateral, syn = syntergum **C** *Cirrospilus cinctithorax*, mesosoma lateral **D** *Pnigalio coloni*, mesosoma, lateral **E** *Aprostocetus hibus*, mesosoma dorsal smg = submarginal grooves **F** *Nesolynx* sp., mesosoma, dorsal.

only at mesocoxal insertion. Transepimeral sulcus straight, extending dorsoventrally. Propodeal callus with 5 setae. Fore wing with postmarginal vein longer than stigmal vein, submarginal vein with 6 setae.

Metasoma with cercal setae subequal in length.

Etymology. Named after Robert Luke Kresslein, a graduate student of systematics at University of California Riverside, because he introduced T.C.D. into the world of chalcidoid wasps and taught her not to be afraid of insects.
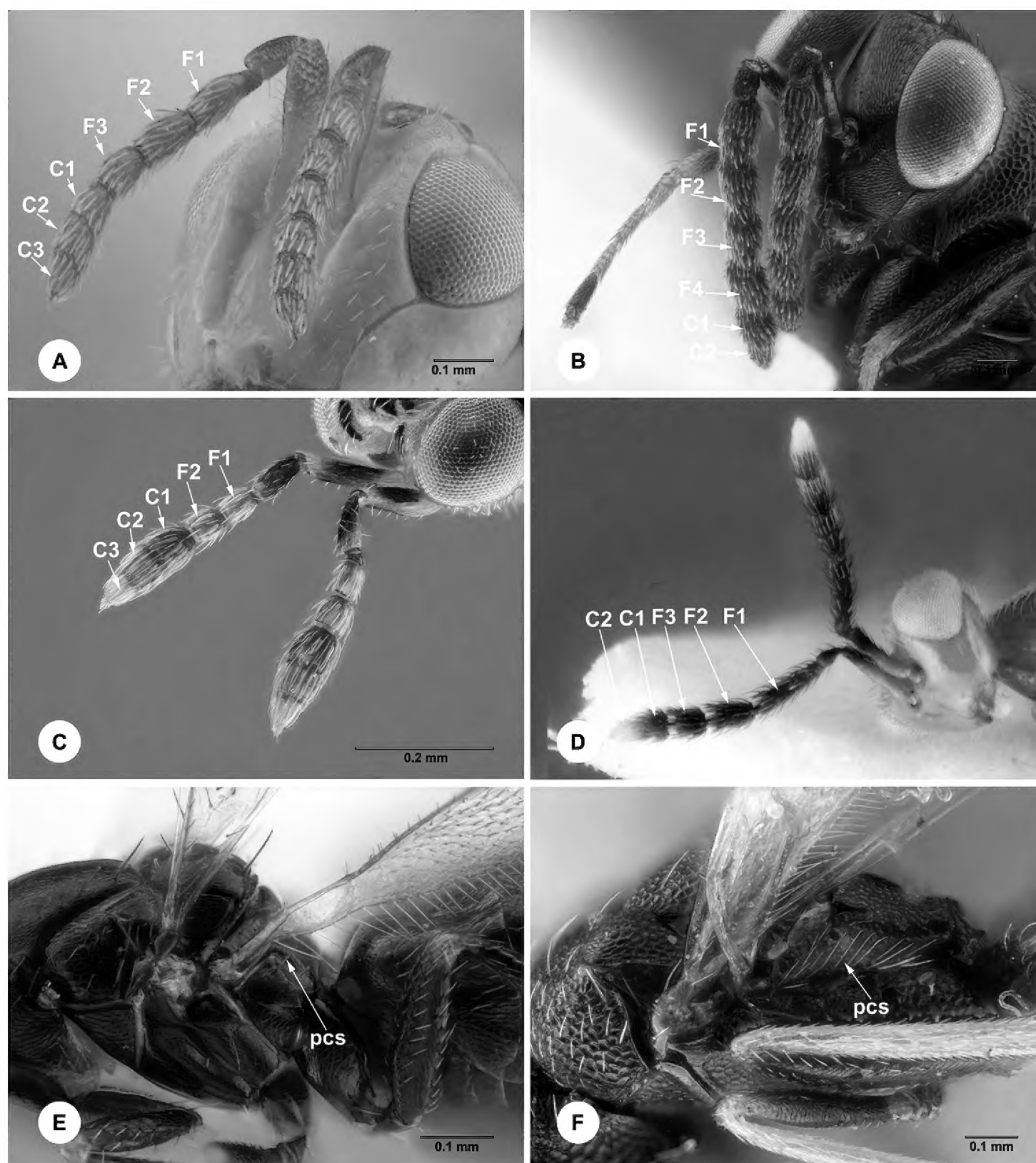
Figure 4. A–F. A *Quadrastichodella* sp., head. F1 = first funicular segment C1 = first clavomere **B** *Sympiesis cf. conica*, head **C** *Burkseus vittatus*, head **D** *Naumanniola* sp. head **E** *Aprostocetus hibus*, mesosoma lateral pcs = propodeal callus setae **F** *Dicladocerus westwoodii*, mesosoma lateral.

Kressleinius celans Domer & Burks, sp. nov.

http://zoobank.org/4174105A-CEAC-467C-8E53-E44F7549E949

Specimen condition. Face obscured by antenna. Propodeum and metanotum obscured by air bubble. Setae on mesoscutellum obscured by debris. Nematoceran fly present as a separate inclusion.
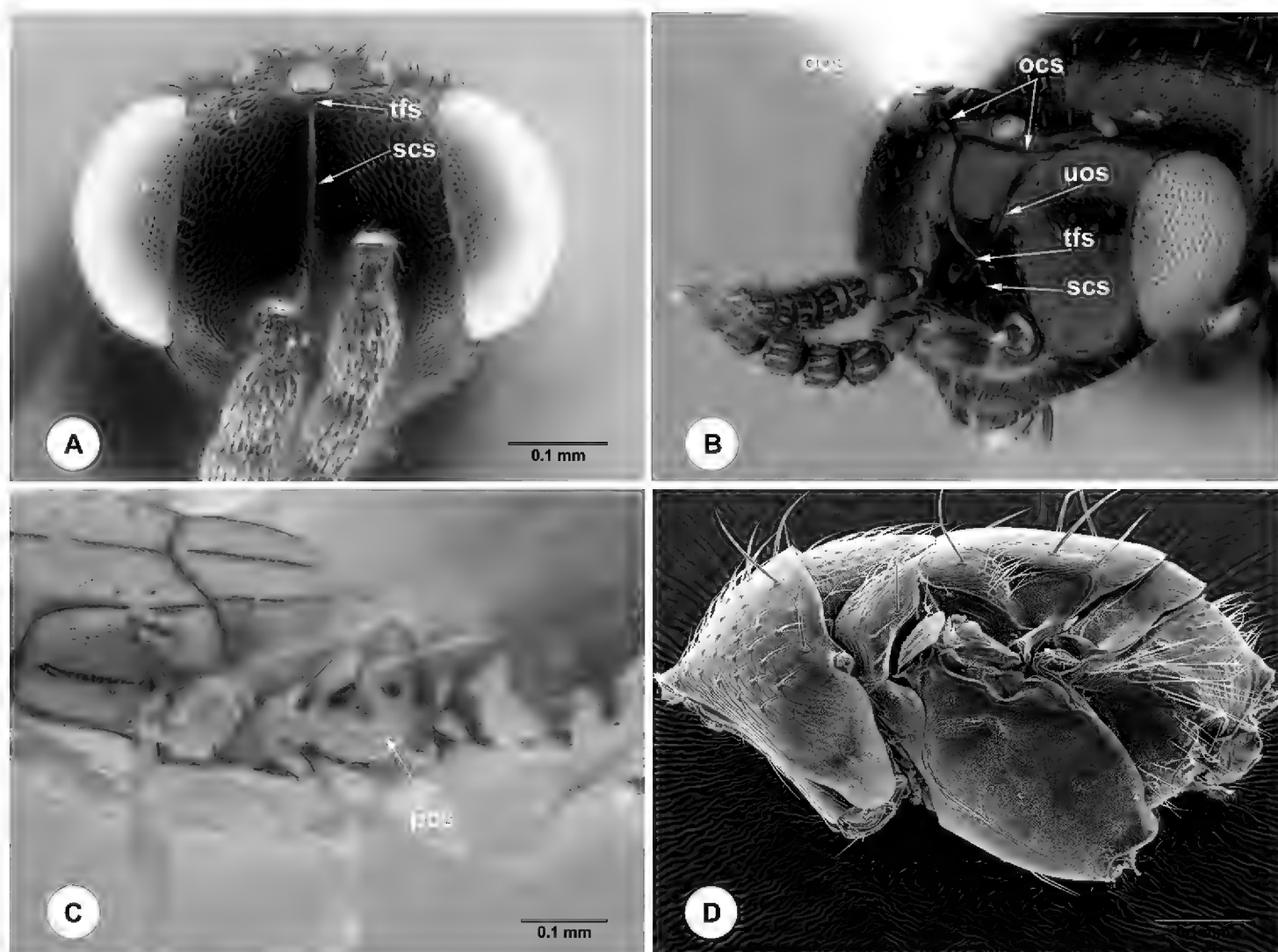
Description. Female: Body length 1.7 mm.

Figure 5. A–D. A *Sympiesis cf. conica*, head, tfs = transfacial sulcus, scs = scrobal sulcus **B** *Crataepus marbis*, head, oos = occellar ocular sulcus, ocs = occellar triangle sulcus, uos = upper ocular sulcus **C** *Zagrammosoma americanum*, mesosoma lateral, pcs = propodeal callus setae **D** *Foersterella erdoesi*, mesosoma, lateral.

Color: head dark, lower part of face pale; flagellum brown with multiporous plate sensillae white; mesosoma dark, mesosomal setae pale; legs pale; gaster with pale lateral markings on metasomal terga 3–6.

Head height 1.4× eye height, sculpture reticulate to imbricate, face alveolate; lateral ocellus not adjacent to eye; eye large; mandible endodont and of normal size. Antenna with first funicular (F1) as long as broad, F2 0.8× as long as broad, F3 0.7× as long as broad; clava 1.2× as long as broad and with apical spine; pedicel without raised sculpture.

Mesosoma length 1.6× its height with reticulate to imbricate sculpture, not flattened. Pronotum without collar; prosternum diamond shaped; propleura diverging; mesoscutum side lobe densely setose and with 1 pair of long posterodorsal setae; mesoscutal midlobe with 2 subparallel rows, distant from notauli, with 3 pairs of small setae anteriorly and 1 large pair posteriorly; dorsellum short (but view distorted by air bubble); propodeum short, without carinae; legs with metatibial spur not elongate.

Fore wing not reduced, 2.1× as long as broad. Relative lengths of costal cell and venation (compared to stigmal vein length): costal cell 3.0, parastigma 1.1, marginal vein 2.4, stigmal vein 1.0, postmarginal vein 1.5; cubital setal line extending from base of wing across speculum.

Metasoma with small, inconspicuous petiole. Gaster length 3.1× as high; hypopygium extending to Mt$_3$; gaster not strongly sclerotized, syntergum present.

Material examined. Baltic amber inclusion. Holotype: female SMNS BB-2847. Deposited in SMNS.

Etymology. The name celans, a Latin participle meaning concealing, was chosen because of the air bubble hiding diagnostic structures on the fossil.

Results of phylogenetic analysis

A phylogenetic analysis was conducted for the purpose of testing the character-based reasoning that supports a placement of *K. celans* in Tetrastichinae. This phylogeny is not meant to reflect the real phylogeny of Eulophidae, in part because most of the key features for such a phylogeny are not visible for the fossil. We recovered 12 most parsimonious trees (MP) with 63 steps from the morphological phylogenetic analysis. The strict consensus tree (Fig. 6) revealed poor resolution, in part because the trees grouped into two islands (Maddison 1991). However, *K. celans* always placed within a monophyletic
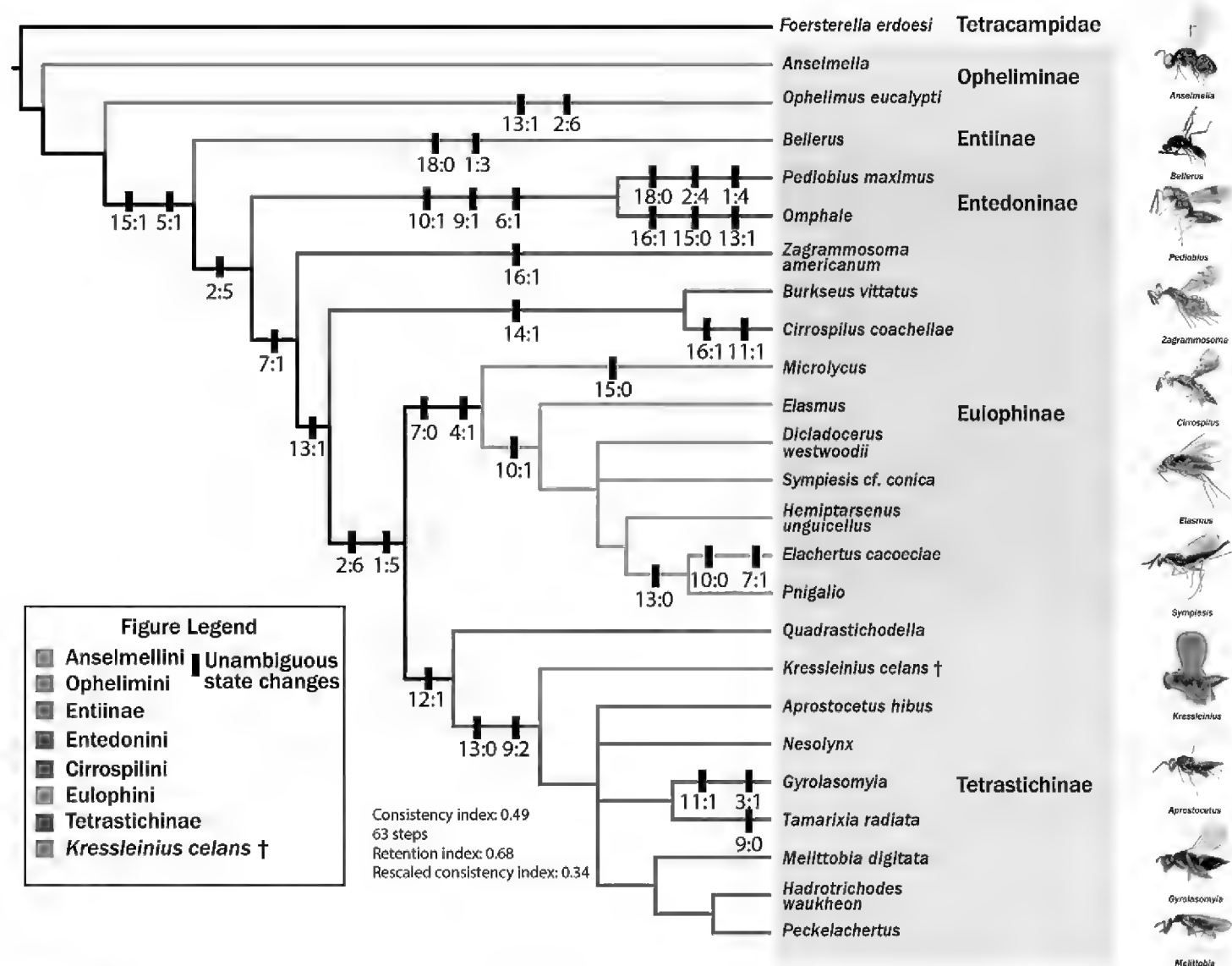

Figure 6. Strict consensus of two of most parsimonious trees based on morphology. Voucher specimens were chosen from those used in ongoing anchored enrichment molecular analyses. Some taxa were added for better coverage of Tetrastichinae. Unambiguous character state changes are plotted with bars.

Tetrastichinae. To increase resolution we used SAW, which retained two MP trees with 63 unweighted steps (retention index 0.68) and thus were part of the set of 12 MP trees. Both topologies placed *K. celans* within Tetrastichinae, supported mainly by 2 unambiguous character state changes: admarginal setae length being short (character 12 state 1), and transepimeral sulcus shape being straight (character 9 state 2). Admarginal setae in more than one row (character 13 state 0) also supported Tetrastichinae, however, this characteristic was homoplastic, shared with some Eulophini. The two trees showed different relationships of *Nesolynx* sp., *Aprostocetus hibus*, and *Melittobia digitata* within Tetrastichinae. In the first tree *Melittobia digitata* was in a polytomy with *Hadrotrichodes waukheon* and *Peckelachertus* sp., with *Aprostocetus hibus* sister to the polytomy. In the other topology, *Melittobia digitata* was the sister group of (*Hadrotrichodes waukheon* + *Peckelachertus* sp.), and *Aprostocetus hibus* was in a polytomy with *Nesolynx* sp., *Gyrolasomyia* sp., and *Tamarixia radiata* formed a clade emerging from a polytomy in both trees.

Discussion

Subfamily placement of *K. celans* was problematic because it has many plesiomorphic characteristics and lacks obvious synapomorphies with major groups of Eulophidae. Therefore, we proceeded to investigate genera both with the distinctive characteristics and those with exceptions. We included specimens from each subfamily to get a better idea of some of the general characteristics. We also used the characteristics from the genera in the phylogenetic analysis, which placed *K. celans* in Tetrastichinae.

Entedoninae possess a reduced basitarsal comb, which is a potential synapomorphy uniting the two tribes Euderomphalini and Entedonini (Gumovsky 2011). Euderomphalini is identifiable in part by an enlarged mesoscutellum and at most 6 flagellomeres, while Entedonini is diagnosed by concealed mesothoracic spiracles. *Kressleinius celans* has an exposed mesothoracic spiracle and an oblique non-reduced basitarsal comb, which excludes placement in Entedoninae. Opheliminae differs from the fossil in many ways, such as having more flagellomeres and placement in Entiinae was also rejected based on the number of funiculars (4–5 in female Entiinae), while *K. celans* has only 3 funiculars (fig. 18).

Eulophinae was the only other subfamily that could not be instantly rejected because *K. celans* shares a reduction in the number of flagellomeres with Eulophinae and many Tetrastichinae. In Eulophinae, there are two tribes: Eulophini, with either 3 funiculars and 3 clavomeres or 4 funiculars and 2 clavomeres, and Cirrospilini with always 5 flagellomeres (2 funiculars and 3 clavomeres, or 3 funiculars and 2 clavomeres). Although some Eulophini have the same flagellomere segmentation as *K. celans*, their propleura shape differs in all genera from *K. celans* except for *Dicladocerus*. Eulophini have the propleura posteriorly straight while in *K. celans* the propleura are diverging posteriorly. *Dicladocerus* also has diverging propleura, but differs from *K. celans* in many other ways, such as having >10 propodeal callus setae and having long admarginal setae in one row. Therefore, placement of *K. celans* in Eulophini was rejected.

Female Cirrospilini have a similar body shape to *K. celans*; however, the fossil differs in having one additional flagellomere past the anelli. Antennae of Cirrospilini are either 2 funicular/3 clavomeres or 3/2, while the fossil is 3/3 like most female Tetrastichinae. Other than antennal reduction, Cirrospilini share plesiomorphic characteristics with Tetrastichinae, such as having submedian grooves on the mesoscutellum, diverging propleura, and complete incised notauli. We discovered a new characteristic for the tribe Cirrospilini: the transepimeral sulcus is either a strong sinuate curve or at least slightly curved, whereas in Eulophini the sulcus is never strongly sinuate or completely straight and in almost all observed Tetrastichinae the sulcus is straight, except for *Quadrastichodella* having a slightly curved suclus. *Kressleinius celans* has a straight transepimeral sulcus, therefore placement in Cirrospilini was rejected, leaving Tetrastichinae as the most reasonable placement for the fossil.

Tetrastichinae appear to have several distinct lineages with their own apomorphies, but the subfamily does not have any single unifying feature. Most Tetrastichinae have a short postmarginal vein, and submedian grooves on the mesoscutellum, but this does not hold true for all genera currently placed in this subfamily (Yoshimoto 1970; LaSalle 1994). *Kressleinius celans* has a long postmarginal vein; we did not observe submedian grooves on the mesoscutellum due to artefacts obscuring most of this body region. Since *K. celans* possesses few typical features of Tetrastichinae we examined lineages with the exceptions to the typical features, such as *Peckelachertus*, *Nesolynx*, and *Quadrastichodella*.

Peckelachertus, *Nesolynx* Ashmead and *Quadrastichodella* (Tetrastichinae) all resemble *K. celans* in different ways. *Peckelachertus* resembles the fossil by having a long postmarginal vein, more than 2 submarginal vein setae, few propodeal callus setae, a straight transepimeral sulcus meeting the pleural sulcus at the metacoxa, and short admarginal setae in more than one row. *Nesolynx* has all of these characteristics except it has a short postmarginal vein and long admarginal setae in more than one row, however it has a large prepectus like *K. celans*. *Quadrastichodella* also has the same characteristics as *Peckelachertus* except for the transepimeral sulcus being slightly curved and the short admarginal setae is in one row but it has markings on the gaster similar to *K. celans*. In addition, numerous genera of Tetrastichinae have a sulcus surrounding the ocellar triangle and extending to the eyes, similar to that of *K. celans*. Based on the morphological comparison with extant species of Eulophidae discussed above and following the results of the phylogenetic analysis we place *K. celans* in Tetrastichinae. This provides the earliest fossil record for one of the most diverse lineages of Chalcidoidea.

Acknowledgements

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